BIOLOGICAL CONSERVATION 141 (2008) 427–437

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

# Restoration of threatened red gorgonian populations: An experimental and modelling approach

*Cristina Linares*[a,b,*], *Rafel Coma*[a], *Mikel Zabala*[c]

[a]*Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés Cala Sant Francesc 14, E-17300 Blanes, Girona, Spain*
[b]*Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim 37-49, E-08003 Barcelona, Spain*
[c]*Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain*

A R T I C L E I N F O

*Article history:*
Received 5 February 2007
Received in revised form
10 October 2007
Accepted 22 October 2007
Available online 11 December 2007

*Keywords:*
Octocorals
*Paramuricea clavata*
Restoration
Transplants
Matrix models
Conservation
Marine protected areas

A B S T R A C T

The increasing disturbances affecting marine communities highlight the need to examine restoration measures that can be added to other conservation efforts for threatened populations. The main goal of this study was to examine the usefulness of ecological restoration in the management of gorgonian populations damaged by diving activity in intensively visited marine protected areas (MPAs). We used field experiments as well as simulations from size-structured matrices to assess the utility of transplantation of living fragments from damaged colonies to increase the viability of threatened populations. Despite results showing that technique failure caused the loss of 40% of transplants, well-attached transplants achieved survival rates (80%) similar to those of natural colonies. Surprisingly, environmental conditions (light level and presence of algae) did not have a significant effect on the mortality of the transplants, but did affect methodological failure rates (37% of transplants were lost in the photophilous treatments in contrast to the 25% lost in sciaphilous treatment). The simulations showed a substantial increase in the annual population growth rate ($\lambda$) only when transplantation was performed every two years and under the most demanding conditions (recovering 75% of the detached colonies and obtaining 3 fragments from each one). Predictions from the size-structured matrix model suggest severe limitations of this technique at larger spatial scales. However, our study confirms the feasibility of this restoration measure to contribute to the recovery of populations in MPAs affected by local disturbances. The experimental and modelling approaches developed here may provide useful guidelines for future studies on the restoration of marine populations.



## 1. Introduction

Current decline of high diversity marine communities, such as coral reefs and kelp forests, due to the increasing frequency and severity of anthropogenic impacts has highlighted the need to implement efficient restoration strategies as a complement to management and conservation of existing populations (Rinkevich, 1995; Lirman and Miller, 2003; Carney et al., 2005; Precht, 2006).

The red gorgonian *Paramuricea clavata* is an important structural species of Mediterranean coralligenous assemblages (Ballesteros, 2006). This long-lived and slow-growing species exhibits demographic parameters in concordance with the dynamics of the community it inhabits (Coma

* *Corresponding author:* Address: Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Accés Cala Sant Francesc 14, E-17300 Blanes, Girona, Spain. Tel.: +34 972 33 6101.
E-mail addresses: clinares@ceab.csic.es (C. Linares), coma@ceab.csic.es (R. Coma), mzabala@ub.edu (M. Zabala).
0006-3207/$ - see front matter 
doi:10.1016/j.biocon.2007.10.012

et al., 1998; 2004; Linares et al., 2007). Among its life-history traits, the red gorgonian displays a delayed sexual maturity and a great annual investment in sexual reproduction that contrasts with the low recruitment rates observed (Coma et al., 1995; 2001). According to the results obtained from size-structured models developed for this species (Linares et al., 2007), these low recruitment rates would be sufficient to ensure the persistence of red gorgonian populations under the low mortality rates observed in natural conditions (Coma et al., 2004).

However, Mediterranean gorgonian species are currently adversely impacted by a wide variety of disturbances that substantially increase their mortality rates above natural levels. Some of these disturbances are of direct anthropogenic origin, such as anchors, fishing nets, divers and contamination (Arnoux et al., 1992; Harmelin and Marinopoulos, 1994; Coma et al., 2004). Others, such as recent mass mortality events (Garrabou et al., 2001; Linares et al., 2005; Coma et al., 2006), appear to be related to climatic anomalies indirectly linked to human activities (Romano et al., 2000).

Managers of marine protected areas (MPAs) must seriously concern themselves with these threats, especially because of an unsolved paradox: although the creation of marine protected areas is a fundamental tool for the conservation of marine habitats (Kelleher and Kenchington, 1992), they tend to attract more tourism and associated recreational activities such as diving that can have a considerable impact on benthic communities (Garrabou et al., 1998; Wielgus et al., 2002; Coma et al., 2004). The problem may be of particular importance in small protected areas because they are often exposed directly to various anthropogenic activities without being adequately sheltered by buffer zones (Schwartz, 1999). The impact of diving has been demonstrated to increase mortality rates of *P. clavata* by a factor of three at the Medes Islands MPA (Coma et al., 2004), an increase that may be threatening the long-term persistence of the population (Linares, 2006). Intense diving activity is present not only at the Medes Islands MPA but at many Mediterranean MPAs (Harmelin and Marinopoulos, 1994; Francour et al., 2001).

The practice of ecological restoration has long been applied to erosion control, reforestation, and habitat and range improvement (Young et al., 2005). Except for a few experimental instances (Weinberg, 1979; Wilkson and Vacelet, 1979), it has only been during the last decade that the science of restoration ecology has started to be applied to marine communities (Ambrose, 1994; Rinkevich, 1995; Edwards and Clark, 1998; Fonseca et al., 2000; Hernandez-Carmona et al., 2000; Epstein et al., 2001; Precht, 2006). The clonal nature of coral species enables recovery from partial mortality (Hughes and Cancino, 1985). While several restoration techniques have been explored to restore damaged coral reefs, most of them are expensive and labor intensive and can result in high mortality of coral transplants (Edwards and Clark, 1998). However, there have been a few examples of successful restoration on a relatively large scale (Guzman, 1991).

Detachments from the substratum, together with injuries, are the main causes of gorgonian mortality (Yoshioka and Yoshioka, 1991; Wahle, 1985; Weinberg, 1978; Coma et al., 2004). Although the recovery of detached colonies might be possible if they succeed in reattaching, a common process in some tropical gorgonians (Lasker, 1990; Coffroth and Lasker, 1998), the ability of *P. clavata* for natural reattachment has proven to be extremely poor (Coma et al., 1995). Therefore, detached colonies accumulating at the bottom of walls and boulders can survive for several months, but finally die from sedimentation and abrasion. The low recruitment rates (Coma et al., 2001) and high post-settlement mortality observed in the red gorgonian *P. clavata* (Linares et al., in press) led us to examine whether transplantation of living colonies may be suitable for the restoration of damaged populations. Furthermore, the availability of numerous detached colonies overcomes the main drawback of restoration that relies on the acquisition of colonies from a donor area (Edwards and Clark, 1998).

Whether restoration is a feasible tool for contributing to the survival of these populations is an important issue for managers involved with the conservation of *P. clavata* populations in most MPAs. Transplant failures can be due to two different causes: a failure of attachment (technique) or post-attachment survival (environmental factors). The search for techniques to attach colonies to the natural substratum that can show high survival rates is a preliminary step in the study of the effectiveness of transplantation as a management tool. The selection of the appropriate technique and the examination of the survival of transplanted colonies, together with previous knowledge about the population dynamics of the species made it possible to use structured matrix models (Caswell, 2001) to simulate and predict the usefulness of transplantation techniques for the enhancement of damaged populations. In particular, size-structured matrices can be used to estimate the amount of transplantation that would be necessary in each case to reach an objective of demographic stability (i.e. an annual population growth rate, $\lambda = 1$; Doak et al., 1994).

Furthermore, the transplantation of colonies to different environmental conditions may contribute to determining the role that biotic and abiotic conditions play on their survival. In this sense, the lack of gorgonian populations in shallow areas with high irradiance suggests that light either directly or indirectly enhances the competitive success of overgrowing algae, hindering the development of red gorgonian colonies (Weinberg, 1978).

Our study was conducted at the Medes Islands, a NW Mediterranean Marine Protected Area that is one of the most affected by recreational diving in the Mediterranean (about 70,000 dives every year in an area of only 32 ha, Coma et al., 2004). The main goals of this study were: first, to examine different transplanting techniques involving low labor effort and low economic cost; second, to estimate the survival of transplanted colonies in relation to the selected technique and to abiotic and biotic factors such as irradiance and competition with algae; and finally, to predict using a matrix model the transplanting effort necessary to obtain values of annual population growth rates ($\lambda$) close to one, ensuring the long-term persistence of these populations. The results obtained in this study allow us to discuss the feasibility of transplantation as a useful management technique at least for small protected areas where both valuable marine biodiversity and intense diving activity interact.

## 2. Materials and methods

The experimental work was carried out at the Medes Islands Marine Protected Area (NW Mediterranean Sea, 42°02′N, 3°13′E), where well-developed populations of *Paramuricea clavata* cover the more exposed vertical sides of rocky walls (Gili and Ros, 1985).

### 2.1. *Transplantation technique*

The first step was to find a usable technique to transplant fragments of surviving colonies found at the bottom of walls. We were looking for two basic prerequisites: low labor effort and low economic cost, since the final objective was to develop a technique that would be easy to perform not only by scientists, but also by volunteers and managers of MPAs working together.

Using a two-component epoxy putty as glue, we first tested the attachment efficiency of three different techniques to install the colony fragments: *raw*, gluing them directly to the putty (Fig. 1a); *tube,* putting the base of the fragment in a plastic tube (as a sheath) 2 cm long to avoid direct contact of live tissue with the putty (Fig. 1b); and *stick*, adding a PVC stick 5 cm long at the side fixing the fragment to it by means of a plastic bridle and adhering the transplant to the bottom with the putty (Fig. 1c). Differences in gorgonian survival between transplant techniques were tested by means of a $\chi^2$ test.

We also planned to test the effect of size on the survival of transplants, by comparing two different sizes of transplants: small (3–10 cm) and large (10–20 cm). However, preliminary assays indicated that large transplants always displayed high losses of attachment regardless of the technique chosen. This was due to the higher resistance of large transplants to water flow, which easily opened a hole at the base of the transplant before the putty solidified. Subsequently, we used small transplants exclusively, since they showed better attachment success.

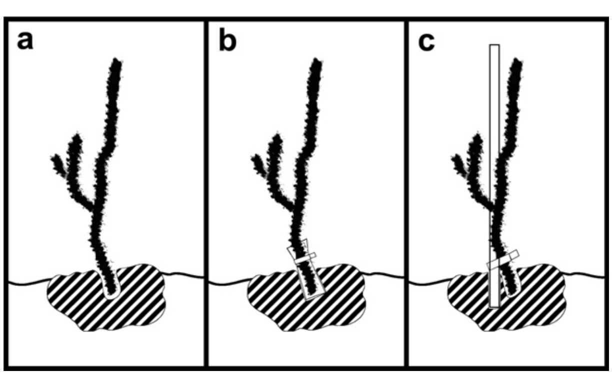


**Fig. 1 – Scheme of the different techniques of gorgonian transplantation used in this study; (a) "raw" technique, fragment transplanted directly to the substrate with epoxy; (b) "tube" technique, fragment transplanted using a plastic tube around the base of the colony to avoid direct contact with the epoxy; (c) "stick" technique, fragment transplanted using a PVC stick to hold up the colony in contact directly with the epoxy.**

To test the success of the different attachment techniques, the transplantation experiment was carried out within a well-developed red gorgonian population at 20–25 m depth. For each technique, 60 fragments between 3 and 10 cm of height were obtained from detached colonies larger than 30 cm recovered at the bottom of walls. The experiment began in June 2001 and the survival of transplanted colonies was monitored monthly during the first four months; after that survival was noted approximately every four months until October 2002.

### 2.2. *Environmental factors*

Once the best transplant technique was selected, we initiated a second experiment to distinguish the role of the main biotic and abiotic factors, such as light and competition with algae, that may contribute to setting the upper limit of the distribution of *P. clavata* (Weinberg, 1978; Ballesteros, 2006). Following the characteristic vertical zonation pattern (i.e. belt-like distribution) of rocky benthic Mediterranean communities (Pérès and Picard, 1964; Gili and Ros, 1985), the upper limit of red gorgonian populations inhabiting steep rocky walls is a clear-cut border parallel to the sea surface (following definite isobaths). On large walls with changes in orientation and irradiance, this pattern is modified and the upper limit of depth distribution of the gorgonians varies in diagonal. This suggests a dependence of the upper depth distribution of red gorgonian colonies on light conditions. At the site studied, this pattern is characterized by having an upper limit that is shallower on the side of the wall facing north and deeper at the side of the wall facing east and south. However, dependence of this pattern on environmental conditions suggests that it may vary by location. Taking advantage of this observed pattern, in April 2002 we started an experiment transplanting colonies with the following experimental design: 20 transplants were installed on the same rocky wall and at the same depth (15–20 m) under three different types of environmental conditions:, (1) in photophilous ambient (with high levels of irradiance) without gorgonians and with algae (at the upper side of the diagonal; Fig. 2a), (2) in photophilous ambient without gorgonians but also without algae (because we removed them during the first six months of the experiment, when the peak of algal growth occurs; Fig. 2b) and, (3) in sciaphilous ambient (with low levels of irradiance), within well-developed gorgonian populations (at the lower side of the diagonal, Fig. 2c). This design was repeated at three different localities (Pedra de Deu, Pota del Llop and Tascons), where well-developed red gorgonian populations can be found (Fig. 2). Survival rates of transplants were compared with those obtained for natural colonies (ranging between 3 and 10 cm) during a study of the population dynamics of this species in the same study area (Linares et al., 2007).

To characterize irradiance at the study sites, light intensity was recorded where the transplants were installed by 2 synchronized HOBO® LI data loggers (Onset Computer) for the two different light environments. Measurements were recorded in lumens feet$^{-2}$. Fig. 3 shows the differences in light conditions at two of the three experimental sites. Despite the fact that the three environmental conditions were located at the same depth, differences in orientation produced a

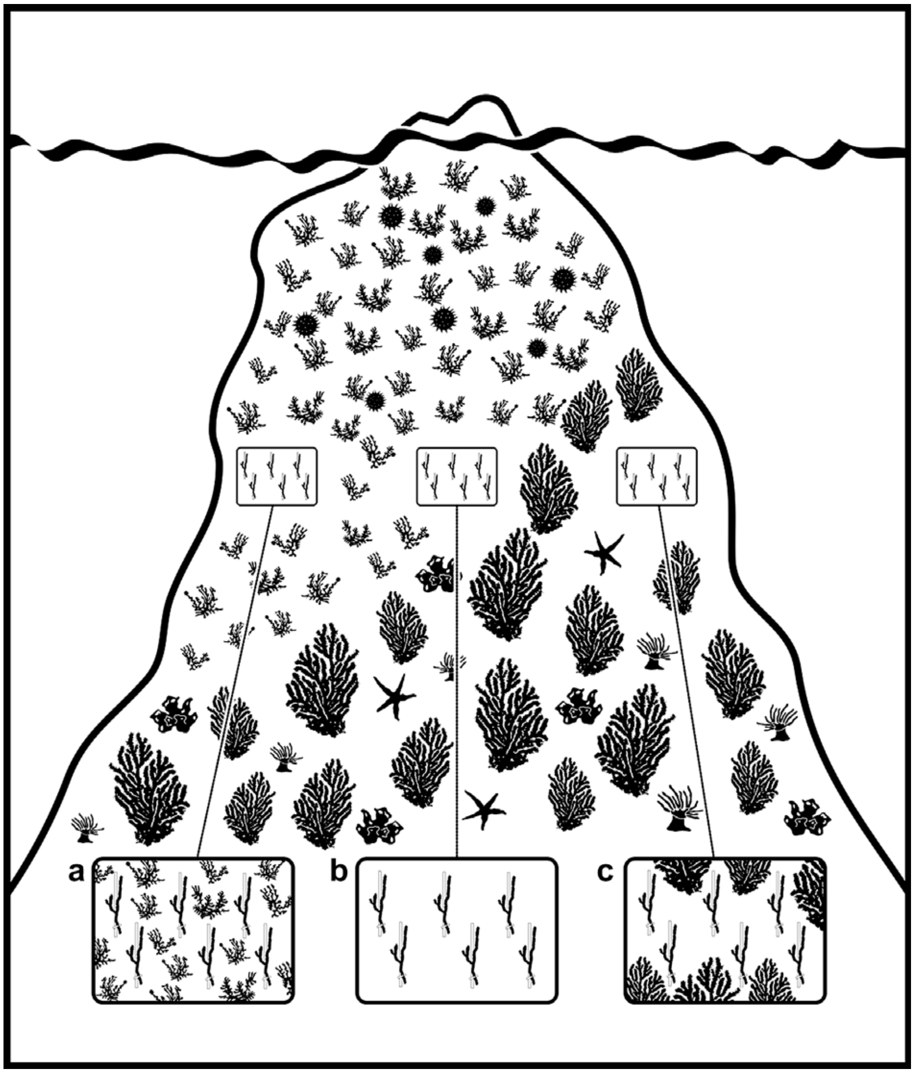


**Fig. 2 – Experimental design of gorgonian transplantation. Note that the oblique border between algal dominated and gorgonian dominated communities allows transplantation at the same depth. (a) Transplants in photophilous ambient with algae. (b) Transplants in photophilous ambient with algae removed. (c) Transplants in sciaphilous ambient.**

tenfold difference in the irradiance reaching transplants at the two photophilous treatment sites in contrast to the sciaphilous site. This difference was examined at the beginning of the experiment (April 2002, Fig. 3).

The survival of transplants was monitored monthly for six months after the beginning of the experiment (from April to October 2002), and from then on, once a year over the following three years (2003, 2004 and 2005). The loss of transplants as well as the death of transplanted colonies was recorded separately during each census in order to distinguish between a failure of the methodology (attachment) and mortality of the transplants. A Kruskall–Wallis test was applied to examine significant differences in the proportion of live, dead and lost transplants between the three experimental treatments.

### 2.3. Modelling approach

In addition to the experimental work, we used a size-structured matrix model to evaluate the transplanting effort that would be necessary to reach the conventional objective of enhancing the annual population growth rate ($\lambda$) to values equal or close to one.

For all simulations we used the average matrix obtained for three annual matrices (between 2001 and 2004) from Medes Islands populations (Table 1). Matrices were constructed using a set of seven age- and size-defined stage classes following the steps detailed in a previous study (Linares et al., 2007). An important factor contributing to the low lambda value obtained for this matrix (0.937, reference lambda) is the estimated three-fold increase in natural mortality caused by the high diving activity at this MPA (Coma et al., 2004).

The transplantation of a colony represents a change from an absolute loss to a new incorporation through a loop in the dynamics of the matrix model. In this loop, the otherwise lost colonies from the size classes 4–7 (10–20 cm, 20–30 cm, 30–40 cm, and >40 cm) would be new incorporations to the chosen transplanted class; i.e. fragments of 3–10 cm (class 3)

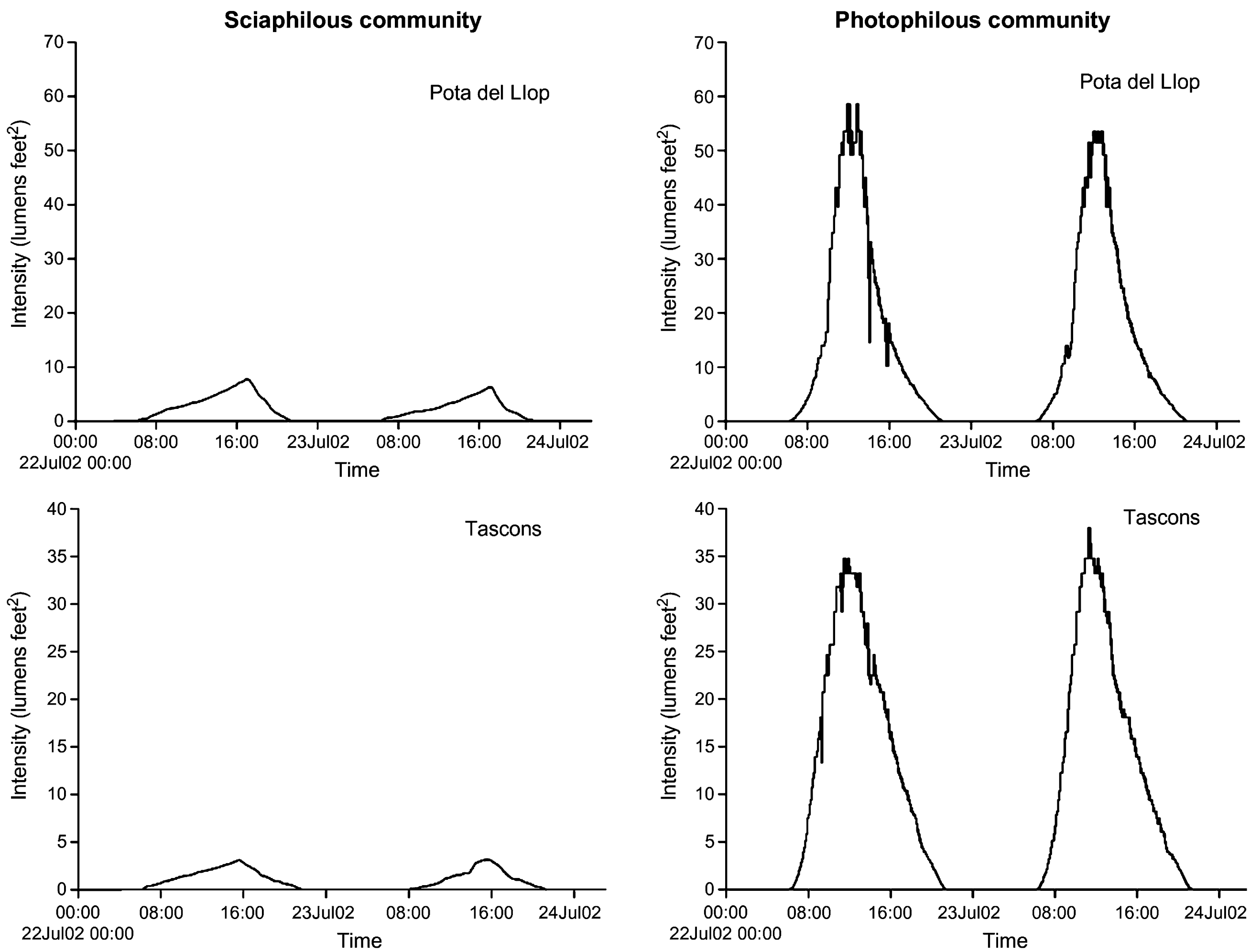


**Fig. 3 – Light intensities recorded at two sites of the Medes Islands (Tascons and Pota del LLop) where the transplantation was performed. Twenty transplants were placed in the two communities where survival was studied (communities under conditions of shade and abundant light) at the same depth (15–20 m) for each site.**

**Table 1 – Average size class transition matrix for the red gorgonian populations at the Medes Island Marine protected area (deterministic lambda (λ) = 0.937; see Linares et al. (2007))**

| Size class $t+1$ | Size class at time $t$ | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| 1 | 0 | 0 | 0 | 0.003 | 0.089 | 0.378 | 0.810 |
| 2 | 0.684 | 0.483 | 0.018 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0.202 | 0.813 | 0.034 | 0 | 0 | 0 |
| 4 | 0 | 0 | 0.087 | 0.833 | 0.057 | 0.020 | 0 |
| 5 | 0 | 0 | 0 | 0.072 | 0.759 | 0.124 | 0.019 |
| 6 | 0 | 0 | 0 | 0 | 0.052 | 0.731 | 0.059 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0.063 | 0.850 |

and fragments of 10–20 cm (class 4) (Fig. 4). Although large transplants experienced a higher proportion of technique failure (see Section 2) than small transplants, simulations were run using both sizes in order to assess whether a higher investment in improving the technique for installing large colonies for future management applications would be worth exploring. Survival rates of natural colonies (ranging between 10 and 20 cm), obtained during a previous study of the population dynamics of this species from the same area (Linares et al., 2007), were used to run these simulations.

Given that transplantation effectiveness relies on the proportion of recovered colonies, the number of fragments and the frequency of transplantation, different simulations were run changing these parameters. We estimated the increase in survival obtained from each simulated transplantation and then added this increase to the right elements of the

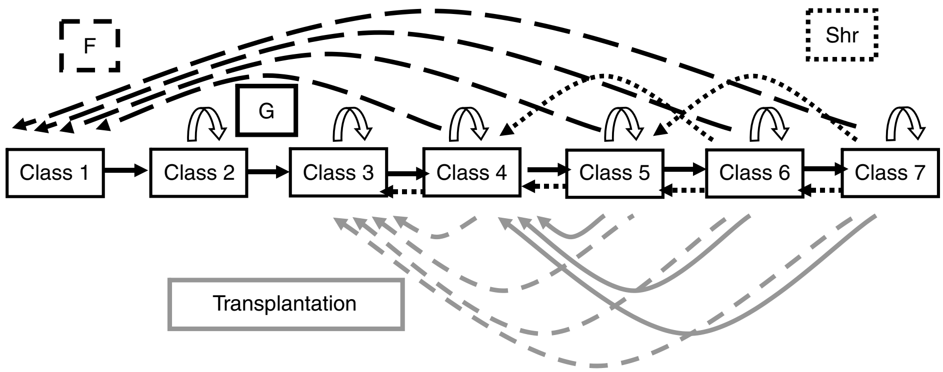


**Fig. 4 – Life cycle graph of the gorgonian *Paramuricea clavata* showing the natural demographic processes (black lines) as well as the transplantation processes (grey lines). G = growth (solid lines), F = fecundity (dashed lines), Shr = shrinkage (dotted lines). First class is an age-based class, Class 2 colonies are at least two years old between 0.3 and 3 cm in height, class 3 colonies are between >3 and 10 cm in height and are pre-reproductive, while classes 4–7 are >10–20 cm, >20–30 cm, >30–40 cm, and >40 cm in height, respectively.**

matrix that benefit from this transplantation, class 3 ($a_{34}$, $a_{35}$, $a_{36}$, $a_{37}$) or class 4 ($a_{45}$, $a_{46}$, $a_{47}$). To run the model we used the transplanted matrix and then the original matrix for the other iterations. We used the stochastic log growth rate using Tuljapurkar's approximation (Morris and Doak, 2002) to choose some matrices more often than others when we simulated different frequencies of transplantation.

During a first step, modelling the minimum effort of transplantation, we simulated the effect of a sole transplantation under the least demanding conditions (one fragment from each recovered colony and 10% of the colonies recovered). In a second step, still with a sole transplantation we simulated the effects of increasing the efficiency of transplantation by means of different combinations of proportion of recovered colonies and the number of fragments obtained from these colonies. The percentage of detached colonies recovered by the transplantation was simulated considering 10%, 25%, 50% and 75% of colonies recovered, and the number of fragments obtained from these colonies was tested using 1, 3 and 5 fragments for transplants of 3–10 cm in height and 1, 2 and 3 fragments for transplants of 10–20 cm. The simulations were performed following the same steps described above. Finally, to test the effect of repeated transplants we used the matrices obtained previously to iterate the transplant matrix with the original matrix with increasing frequency over time, testing a single transplantation every 100 years, 10 years, 5 years, 3 years, 2 years and 1 year, respectively.

## 3. Results

### 3.1. *Technique: Attachment success*

The use of a PVC stick to attach the transplanted gorgonian to the rocky substrata provided the highest rate of survival of all the techniques examined (Fig. 5). With this technique 70% of transplanted colonies survived beyond one year, while survival using the "tube" technique was only 50%. With the "raw" technique, direct attachment of the colonies to the substrata, only 30% of colonies lived until October 2002. Although differences among the three transplant techniques were not significant ($\chi^2 = 3.300$, d.f. = 2, $p = 0.192$), we selected the "stick" technique because it displayed the highest rate of survival throughout the entire experiment (Fig. 5).

### 3.2. *Environmental factors*

The comparison between the survival of transplants under the three different experimental conditions assayed (sciaphilous, photophilous with algae, and photophilous without algae) and the observed survival for natural (non-transplanted, Table 1) colonies is shown in Fig. 6. The decrease of survival includes both causes of mortality: failure of attachment and death. In general, survival under the three environmental conditions displayed a similar temporal pattern in which two phases can be distinguished: a strong decrease during the first year-and-a-half of the study (between April 2002 and October 2003), much higher than the expected natural mortality, and

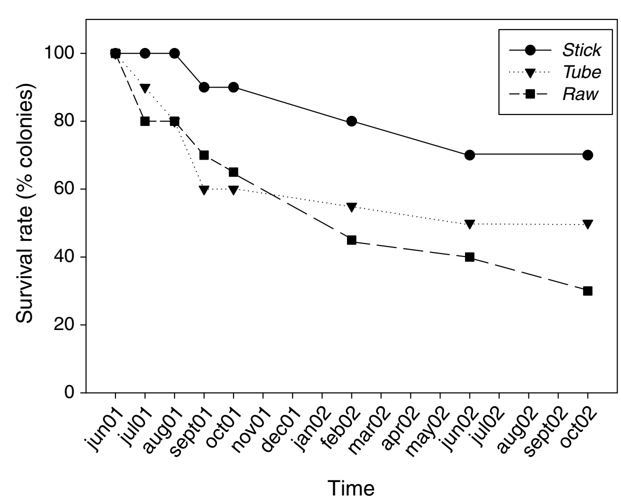


**Fig. 5 – Transplant survival for the three techniques during the first year of the study (from June 2001 to October 2002). Transplants were surveyed each month during the first four months and, thereafter, every four months. Data are shown as a percentage of the 20 original transplants for each technique.**

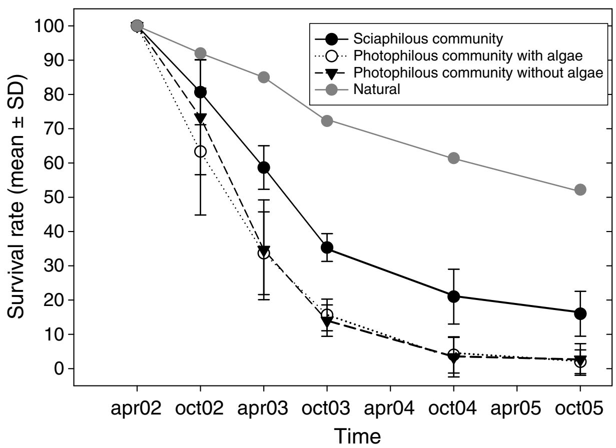


**Fig. 6 – Transplant survival under the three experimental treatments and non-transplanted colonies survival from April 2002 to October 2005. Data are shown as a percentage of the 20 original transplants located in three different replicates, means ± SD was estimated averaging the three replicates for each treatment (*N* total = 60 for each treatment).**

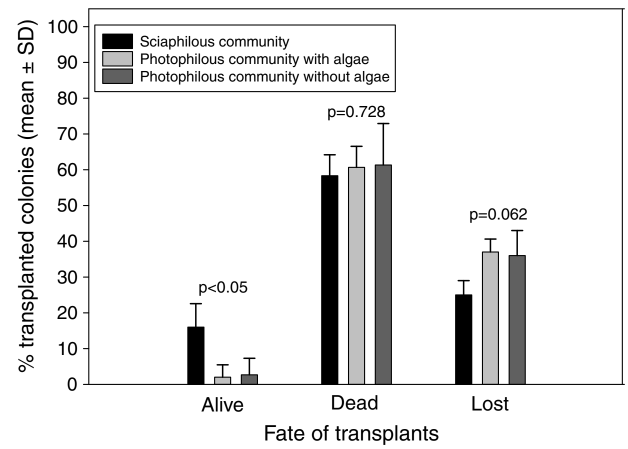


**Fig. 7 – Fate of the transplanted colonies (%) divided into "surviving" transplants, "dead" transplants due to a natural mortality, and "lost" transplants due to a technique failure. The SD was estimated averaging the three localities where we performed each treatment. P values are from a Kruskal–Wallis test comparing the effect of treatment on the percentage of colonies surviving, dead and lost.**

a second phase during which survival was similar to natural values excluding the lost transplants (80% and 85% transplant survival and natural survival respectively, see Table 1). Nevertheless, after three years (October 2005), survival of transplants in sciaphilous communities was only 16% compared with 52% for non-transplanted colonies.

Comparison between the three experimental treatments showed that one year after the beginning of the experiment (April 2003) transplanted colonies within their typical sciaphilous community exhibited the highest level of survival (58% vs. 34% for both photophilous treatments). At the end of the study, survival of transplants in the sciaphilous community remained higher than the colonies transplanted in photophilous conditions (Kruskal–Wallis, $p = 0.042$).

After that the colonies transplanted to high levels of irradiance showed similar survival rates regardless of exposure to competition with algae (Fig. 6). At the beginning of the experiment (between April and October 2002), survival of the transplanted colonies in an environment with abundant light and without algae was higher than in the environment with abundant light and presence of algae (73% vs. 63% survival, respectively). This time period coincided with the period of maximum algal growth. However, three years after the beginning of the experiment, only about 2% of the transplants survived in the two areas exposed to abundant light (Fig. 6).

In order to examine the causes of mortality (technique or environmental), we compared the fate of transplants, distinguishing between live, dead and lost transplants (Fig. 7). Unexpectedly, the differences in survival between treatments were due to differences in the success of attachment (lost transplants) despite using the same technique. Although no significant differences were found between treatments (Kruskal–Wallis, $p = 0.062$), results showed a trend toward a higher proportion of lost colonies in the photophilous treatments (37% and 36%) than in the sciaphilous treatment (25%). These losses mainly occurred during the first year of the transplantation (Fig. 6). In contrast, the number of dead transplants was similar under both sciaphilous or photophilous conditions (ranging between 58% and 61%; Fig. 7)

### 3.3. *Modelling approach*

Simulations were conducted on the basis of survival rates of well-attached transplants that do not differ from natural values (see above). The simulations of a single transplantation

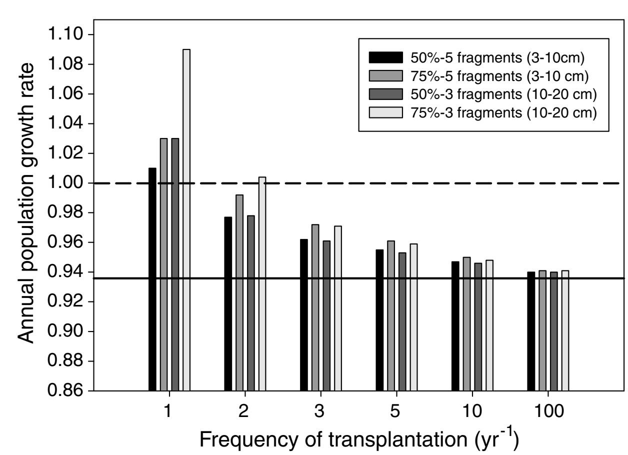


**Fig. 8 – Effect of transplantation frequency on the annual population growth rates. Six frequencies (a single transplantation every 100 years (1/100 years), 1/10 years, 1/5 years, 1/3 years, 1/2 years and 1/1 year are represented using the highest efficiencies on both number of fragments and percentage of recovered colonies for the two transplants sizes. Black line represents the reference lambda value ($\lambda = 0.937$). Dashed line represents the long-term population persistence of the population ($\lambda = 1$).**

with increasing efficiencies did not substantially modify the lambda values (Fig. 8, see results for a single transplantation every 100 years). In contrast, if the transplantation was periodically repeated, significant increases in lambda were observed. However, lambda values close to one were achieved only with high transplantation efficiency (i.e. transplanting on the order of 75% of the detached colonies, and obtaining at least 3 fragments per colony) and high transplantation frequency (at least one every two years).

Fig. 9 shows the positive effect on the lambda values of increasing the efficiency through the proportion of recovered colonies and the number of transplants obtained from them at the maximum frequency of transplantation (every year). Both transplant sizes exhibited a similar pattern of lambda increase with an increasing proportion of recovered colonies. Although all the simulations showed an improvement with respect to the reference lambda, the lambda values were close to or higher than 1 only when over 50% of the detached colonies were recovered and more than one fragment was obtained per colony for both sizes of transplants (Fig. 9a and b).

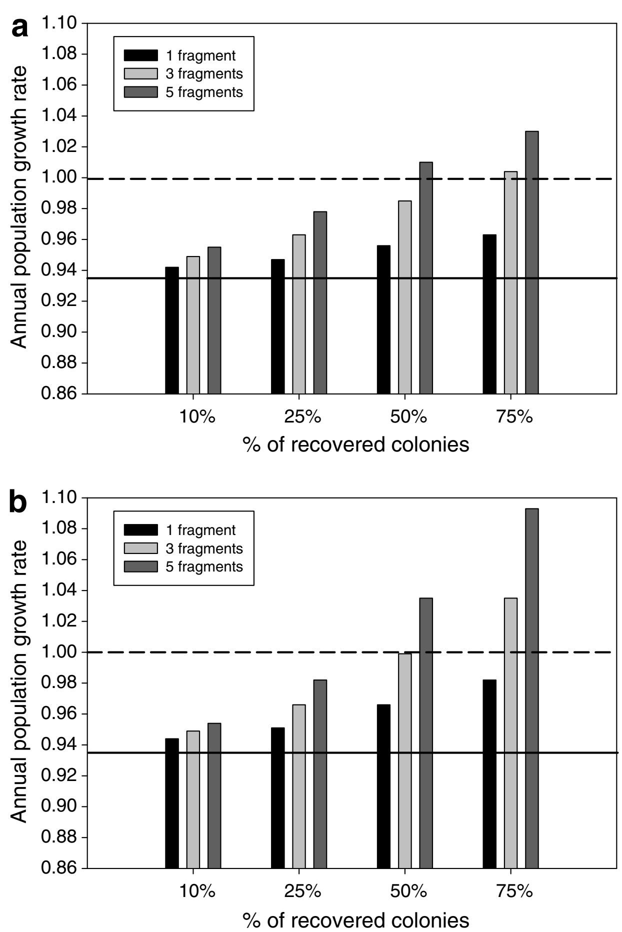


**Fig. 9 – Annual population growth rates ($\lambda$) obtained with transplantation repeated each year. Simulations were performed simultaneously changing the percentage of recovered dead colonies (detached colonies from the substratum) and the number of fragments obtained from recovered colonies through the transplantation of fragments of two size-classes. (a) Transplants of 3–10 cm. (b) Transplants of 10–20 cm. Black line represents the reference lambda value ($\lambda$ = 0.937). Dashed line represents the long-term population persistence of the population ($\lambda$ = 1).**

## 4. Discussion

### 4.1. *Transplantation technique*

During the technique-related experiment performed within the gorgonian community, the relatively high survival (almost 70%) obtained with the "stick" technique indicated that this technique might enable successful transplantation. In the environmental-related experiment, technique failure was an important cause of mortality (over 40% of transplanted colonies were lost), due mainly to either a break in the epoxy/substratum attachment or the loss of the stick due to poor installation.

After an initial period of attachment failure, well-attached transplants had survival rates similar to those of natural colonies. The contrast between the losses due to attachment and the survival of well-attached transplants shows two different phases. In the first phase (before 2003), the mortality due to attachment failure was much higher than under natural conditions, but in the second phase (after 2003) the slopes displayed by all treatments were similar to that exhibited by natural colonies. Although this result may be considered satisfactory enough to qualify the transplantation method as a feasible management tool, our study has revealed some uncertain aspects of marine restoration and demonstrates that some degree of failure should be expected, as other authors have indicated (Edwards and Clark, 1998; Yap, 2000; Carney et al., 2005). Improvement of the technique for the initial installation of transplants on the substratum should be the primary goal of future studies on transplantation of gorgonians.

### 4.2. *Effects of environmental conditions on colony survival*

Surprisingly, environmental conditions did not have a significant effect on mortality of the transplants, but did influence methodological failure. The differences between the sciaphilous and photophilous communities were due more to the higher number of technical losses on the photophilous treatment than to the process of competition or to differences in irradiance that we expected to affect the survival of the transplanted colonies. One possible explanation for these unexpected results could be the difference in intensity of water flow that the transplants experienced under different treatments. As water movement depends very much on depth (Ballesteros and Zabala, 1993), we would expect the same water flow in both treatments. Nevertheless, at a finer scale, the cover provided by the gorgonian forest (sciaphilous treatment) to the transplants decreased water movement between 20% and 40% (M. Ribes, unpublished data), which may have contributed to the improved success of transplants. The likely influence of water movement on transplantation success merits further investigation.

### 4.3. Modelling

Three main facts lead us to consider small transplants as the best size for transplantation. First, preliminary experiments pointed out that large transplants exhibited a higher technique failure presumably because of their higher resistance to water flow. Second, simulations did not exhibit a substantial difference in lambda values between the two transplant sizes. This agrees with previous experimental studies, which did not observe big differences between transplant sizes (Lewis, 1991; Yap et al., 1998). Third, the use of large transplants would require a higher investment in the installation technique to reduce attachment failure.

The efficacy of transplantation could be improved by both recovering more colonies and splitting those colonies into more fragments. A large damaged colony found on the sea bottom can be split into small healthy fragments for transplantation. Obviously, the number of resulting fragments is positively related to the size of the damaged gorgonian and negatively related to the size of the transplant. The total number of detached gorgonians found and recovered depends on the magnitude of the surveillance effort. Finally, effectiveness can also be improved by repeating the transplantation at increasing frequencies (from one-time transplantation to annual transplantation). Our simulations showed that under the current high rates of mortality due to the influence of diving a single transplantation followed by the same measures of management had no effect on the viability of this population. The annual population growth rate improved substantially only after increasing the frequency of transplantation. *P. clavata* populations continued to decline ($\lambda < 1$) unless the transplantation was performed every 2 years under the most demanding conditions, (i.e., recovering 75% of the detached colonies and obtaining three fragments of each). Even if transplantation was performed yearly, it was necessary to recover more than 50% of the colonies and to obtain more than one fragment from each of them to reach the objective of "population persistence" ($\lambda = 1$).

### 4.4. Transplantation and conservation of threatened populations

Managers of MPAs are concerned about the different kinds of disturbances that are currently affecting the coralligenous community (see Section 1). Predictions from the matrix models suggest severe limitations to transplantation at a large spatial scale. Therefore, the transplantation method appears to be unable to counteract the high mortalities displayed by recent mass mortality events (Cerrano et al., 2000; Perez et al., 2000; Garrabou et al., 2001), where on the order of half of the population has been lost (Linares et al., 2005; Coma et al., 2006). However, the results indicate that transplantation could be a viable method to contribute to the recovery of populations in MPAs locally affected by disturbances (i.e. diving activity, anchors, fishing nets and contamination). As has been proposed for other coral species, restoration strategies can rescue reefs from the on-going impacts of human activities and be used as a supplementary management approach for rehabilitation of small and exploited MPAs (Epstein et al., 2001; 2005).

Nevertheless, our study should probably not be considered as representative of conditions common to red gorgonians along the Mediterranean coast. The high level of diving activity at the Medes Islands MPA causes extremely high mortality rates (Coma et al., 2004) that probably require a disproportionately strong transplantation effort and repetition to guarantee population persistence. Given the time and effort required for any transplantation, restoration actions at this MPA should be considered in conjunction with other conservation efforts designed to attenuate the impact of diving (Coma et al., 2004; Linares, 2006). In this sense, the first management strategy to reduce damage to gorgonians should be prevention, through diver education designed to promote good diving practices, as has been suggested for coral reefs with high diving activity (Zakai and Chadwick-Furman, 2002; Baker and Roberts, 2004).

The experimental and modelling approaches developed in this study have provided some clear-cut results that can help managers and scientists to estimate the advisability and utility of this restoration technique. Modelling studies have shown that the current frequency of disturbances may endanger population viability (Linares, 2006) due to the limited ability to recover from injuries and the low level of recruitment displayed by this species (Coma et al., 2001; Linares et al., 2005). In long-lived species such as gorgonians with rare and episodic successful recruitments (Garrabou and Harmelin, 2002) restoration may contribute to the re-establishment of the lost link in the recruitment chain and therefore ensure population persistence.

## Acknowledgments

We thank D. Diaz and B. Hereu for their invaluable assistance in the field, T. García-Rubies for his advice on the experimental design of the study and J. Garrabou for his valuable comments on different versions of the manuscript. We are grateful to D. Doak for all his assistance and patience during the introduction to demographic models and to J. Santiago for figure processing. J. Romero and P. Renom kindly provided the light data loggers. This study was funded by a research Grant CTM2004-03120/MAR from the "Ministerio de Educación y Ciencia" of Spain.

## REFERENCES

Ambrose, R.F., 1994. Mitigating the effects of a coastal power-plant on a kelp forest community-rationale and requirements for an artificial reef. Bulletin Marine Science 55, 694–708.

Arnoux, A., Harmelin, J.G., Monod, J.L., Romaña, L.A., Zibrowius, H., 1992. Altérations de peuplements benthiques de roches profondes en Méditerranée nord-occidentale: quelques aspects biologiques et molysmologiques. Comptes rendus de l'Acadèmie des Sciences III 314, 219–225.

Baker, N.H.L., Roberts, C.M., 2004. Scuba diver behaviour and the management of diving impacts on coral reefs. Biological Conservation 120, 481–489.

Ballesteros, E., 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanography and Marine Biology: An Annual Review 44, 123–195.

Ballesteros, E., Zabala, M., 1993. El bentos: el marc físic. In: Alcocer, J.A., et al. (Eds.), Història Natural de l'Arxipèlag de Cabrera, Monografies de la Societat d'Història Natural de Balears 2, Palma de Mallorca, Spain. pp. 663–685.

Carney, L.T., Waaland, J.R., Klinger, T., Ewing, K., 2005. Restoration of the bull kelp *Nereocystis luetkeana* in nearshore rocky habitats. Marine Ecology Progress Series 302, 49–61.

Caswell, H., 2001. Matrix Population Models: Construction, Analysis, and Interpretation, second ed. Sinauer Associates, Sunderland, Massachusetts, USA.

Cerrano, C., Bavestrello, G., Bianchi, C.N., Cattaneo-Vietti, R., Bava, S., Morganti, C., Morri, C., Picco, P., Sara, G., Schiaparelli, S., Siccardi, A., Sponga, F., 2000. A catastrophic mass-mortality episode of gorgonians and other organisms in the Lig urian Sea (NW Mediterranean), summer 1999. Ecology Letters 3, 284–293.

Coffroth, M.A., Lasker, H.R., 1998. Population structure of a clonal gorgonian coral: the interplay between clonal reproduction and disturbance. Evolution 52, 379–383.

Coma, R., Zabala, M., Gili, J.M., 1995. Sexual reproductive effort in the Mediterranean gorgonian *Paramuricea clavata*. Marine Ecology Progress Series 117, 185–192.

Coma, R., Ribes, M., Zabala, M., Gili, J.M., 1998. Growth in a modular colonial marine invertebrate. Estuarine, Coastal, and Shelf Science 47, 459–470.

Coma, R., Linares, C., Pola, E., Zabala, M., 2001. Seguiment temporal de la gorgònia *Paramuricea clavata* de les illes Medes. In: Zabala, M. (Ed.), Seguiment Temporal de l'àrea Marina Protegida de les illes Medes, Informe anual any 2001, Departament de Medi ambient, Generalitat de Catalunya, Barcelona, Spain.

Coma, R., Pola, E., Ribes, M., Zabala, M., 2004. Long-term assessment of the patterns of mortality of a temperate octocoral in protected and unprotected areas: a contribution to conservation and management needs. Ecological Applications 14, 1466–1478.

Coma, R., Linares, C., Ribes, M., Diaz, D., Garrabou, J., Ballesteros, E., Zabala, M., 2006. Consequences of a mass mortality event on the populations of the gorgonian *Eunicella singularis* (Cnidaria: Octocorallia) in Menorca (Balearic Islands, NW Mediterranean). Marine Ecology Progress Series 327, 51–60.

Doak, D., Kareiva, P., Klepteka, B., 1994. Modeling population viability for the desert tortoise in the Western Mojave desert. Ecological Applications 4, 446–460.

Edwards, A.J., Clark, S., 1998. Coral transplantation: a useful management tool or misguided meddling? Marine Pollution Bulletin 37, 474–487.

Epstein, N., Bak, R.P.M., Rinkevich, B., 2001. Strategies for gardening denuded coral reef areas: the applicability of using different types of coral material for reef restoration. Restoration Ecology 9, 432–442.

Epstein, N., Vermeij, M.J.A., Bak, R.P.M., Rinkevich, B., 2005. Alleviating impacts of anthropogenic activities by traditional conservation measures: can a small reef reserve be sustainedly managed? Biological Conservation 121, 243–255.

Fonseca, M.S., Julius, B., Kenworthy, W.J., 2000. Integrating biology and economics in seagrass restoration: how much is enough and why? Ecological Engineering 15, 227–237.

Francour, P., Harmelin, J.G., Pollard, D., Sartoretto, S., 2001. A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquatic Conservation: Marine Freshwater Ecosystem 11, 155–188.

Garrabou, J., Harmelin, J.G., 2002. A 20-year study on life-history traits of a harvested long-lived temperate coral in the NW Mediterranean: insights into conservation and management needs. Journal of Animal Ecology 71, 966–978.

Garrabou, J., Sala, E., Arcas, A., Zabala, M., 1998. The impact of diving on rocky sublittoral communities: a case study of a bryozoan population. Conservation Biology 12, 302–312.

Garrabou, J., Perez, T., Sartoretto, S., Harmelin, J.G., 2001. Mass mortality event in red coral *Corallium rubrum* populations in Provence region (France, NW Mediterranean). Marine Ecology Progress Series 217, 263–272.

Gili, J.M., Ros, J., 1985. Study and cartography of the benthic communities of Medes Islands (NE Spain). Pubblicazzioni della Stazione Zoologica di Napoli I: Marine Ecology 6, 219–238.

Guzman, H.M., 1991. Restoration of coral reefs in Pacific Costa Rica. Conservation Biology 5, 189–195.

Harmelin, J.G., Marinopoulos, J., 1994. Population structure and partial mortality of the gorgonian *Paramuricea clavata* (Risso) in the Northwestern Mediterranean (France, PortCros Island). Marine Life 4, 5–13.

Hernandez-Carmona, G., Garcia, O., Robledo, D., Foster, M., 2000. Restoration techniques for *Macrocystis pyrifera* (Phaeophyceae) populations at the southern limit of their distribution in Mexico. Botanica Marina 43, 273–284.

Hughes, R.N., Cancino, J.M., 1985. An ecological overview of cloning in metazoan. In: Jackson, J.B.C., Buss, L.W., Cook, R.E. (Eds.), Population Biology and Evolution of Clonal Organisms. Yale Univ. Press, New Haven, pp. 153–186.

Kelleher, G., Kenchington, R., 1992. Guidelines for Establishing Marine Protected Areas. A Marine Conservation and Development Report, IUCN, Gland, Switzerland.

Lasker, H.R., 1990. Clonal propagation and population dynamics of a gorgonian coral. Ecology 71, 1578–1589.

Lewis, J.B., 1991. Testing the coral fragment and size-dependent survivorship hypothesis for the calcareous hydrozoan *Millepora complanata*. Marine Ecology Progress Series 112, 119–128.

Linares, C., 2006. Population ecology and conservation of a marine long-lived species: the red gorgonian *Paramuricea clavata*. Ph.D. Thesis, University of Barcelona.

Linares, C., Coma, R., Diaz, D., Zabala, M., Hereu, B., Dantart, L., 2005. Immediate and delayed effects of a mass mortality event on gorgonian population dynamics and benthic community structure in the NW Mediterranean Sea. Marine Ecology Progress Series 305, 127–137.

Linares, C., Doak, D., Coma, R., Diaz, D., Zabala, M., 2007. Life history and population viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. Ecology 88, 918–928.

Linares, C., Coma, R., Mariani, S., Diaz, D., Hereu, B., Zabala, M, in press. Early life history of the Mediterranean gorgonian *Paramuricea clavata*: implications for population dynamics. Invertebrate Biology.

Lirman, D., Miller, M.W., 2003. Modeling and monitoring tools to assess recovery status and convergence rates between restored and undisturbed coral reefs habitats. Restoration Ecology 11, 448–456.

Morris, W.F., Doak, D.F., 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Pérès, J.M., Picard, J., 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. Recueil des Travaux de la. Station Marine d'Endoume 31, 5–137.

Perez, T., Garrabou, J., Sartoretto, S., Harmelin, J.G., Francour, P., Vacelet, J., 2000. Mortalité massive d'invertébrés marins: un événement sans précédent en Méditerranée nord-occidentale. Comptes rendus de l'Acadèmie des Sciences III 323, 853–886.

Precht, W.F., 2006. Coral Reef Restoration Handbook. CRC Press, Taylor & Francis Group, Boca Raton, Florida, USA.

Rinkevich, B., 1995. Restoration strategies for coral reef damaged by recreational activities: the use of sexual and asexual recruits. Restoration Ecology 3, 241–251.

Romano, J.C., Bensoussan, N., Younes, W.A.N., Arlhac, D., 2000. Anomalies thermiques dans les eaux du golfe de Marseille durant l'été 1999. Une explication partielle de la mortalité d'invertébrés fixés. Comptes Rendus de l'Acadèmie des Sciences Paris III 323, 415–427.

Schwartz, M.W., 1999. Choosing the appropriate scale of reserves for conservation. Annual Reviews of Ecology and Systematics 30, 83–108.

Wahle, C.M., 1985. Habitat-related patterns of injury and mortality among Jamaican gorgonians. Bulletin of Marine Science 37, 905–927.

Weinberg, S., 1978. Mediterranean octocorallian communities and the abiotic environment. Marine Biology 49, 41–57.

Weinberg, S., 1979. Transplantation experiments with Mediterranean gorgonians. Bijdragen tot de Dierkunde 49, 31–41.

Wielgus, J., Chadwick-Furman, N.E., Dubinsky, Z., Shechter, M., Zeitouni, N., 2002. Dose-response modeling of recreationally important coral reef attributes: a review and potential application to the economic valuation of damage. Coral Reefs 21, 253–259.

Wilkson, C.R., Vacelet, J., 1979. Transplantation of marine sponges to different conditions of light and current. Journal of Experimental Marine Biology and Ecology 37, 91–104.

Yap, H.T., 2000. The case for restoration of tropical coastal ecosystems. Ocean and Coastal Management 43, 841–851.

Yap, H.T., Alvarez, R.M., Custodio, H.M., Dizon, R.M., 1998. Physiological and ecological aspects of coral transplantation. Journal of Experimental Marine Biology and Ecology 229, 69–84.

Yoshioka, P.M., Yoshioka, B.B., 1991. A comparison of the survivorship and growth of shallow-water gorgonian species of Puerto Rico. Marine Ecology Progress Series 69, 253–260.

Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters 8, 662–673.

Zakai, D., Chadwick-Furman, N.E., 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biological Conservation 105, 179–187.